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THERMOTROPISM OF ROOTS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 192

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(WITH SIX FIGURES)

I. The thermotropic curvatures of certain roots at temperatures from 10° to 40° C.

II. The changes in permeability of these roots caused by change in temperature from 10° to 40° C.

Introduction

Our knowledge of thermotropism is in a somewhat confused state. We know little about the thermotropic response of stems. A few scattered observations have been made, indicating that stem tips turn toward the source of heat at low temperatures and away from it at high temperatures. More exact investigations have been made of the thermotropic curvatures of roots, but here there seems to be no uniformity of behavior. Under the influence of unequal temperature on two sides, the roots of different species react differently. Some roots give positive curvatures at low temperatures and negative at high temperatures; others show only positive curvatures, and still others give only negative curvatures. It was with the purpose of clearing up these apparent discrepancies and the hope of finding the physical mechanism of the curvatures that the present investigation was undertaken.

Thermotropic curvatures of roots

LITERATURE

The two important papers on thermotropism of roots are WORTMANN'S (10) and KLERCKER'S (2). WORTMANN investigated four species: *Ervum lens*, *Pisum sativum*, *Zea Mays*, and *Phaseolus multiflorus*. He concluded that roots have positive thermotropism at low temperatures and negative at high tempera-

tures, that is, above 35° or 40° C. The one exception he found was *Phaseolus multiflorus*, which gave negative curvatures from 22° to 50° C., but no curvature below 22° . The secondary roots of *P. multiflorus* reacted positively at low and negatively at high temperatures. WORTMANN thought, therefore, that the primary roots must have a positive thermotropism, although he was not able to demonstrate it.

AF KLERCKER studied *Pisum sativum*, *Helianthus annuus*, *Faba vulgaris*, and *Sinapis alba*. In the first three species he observed only negative thermotropism; while *Sinapis alba* gave positive curvatures from 14° to 29° C., and no curvatures at the higher temperatures. PORODKO (7) studied the thermotropic curvatures of roots at temperatures from 40° to 70° C. He obtained negative curvatures and thought therefore that roots have only negative thermotropism.¹

INVESTIGATION

Method.—The apparatus used is a modification of GANONG'S differential thermostat.² A zinc trough, 20 inches long, having a zinc box attached at each end, was heated at one end by an electric coil and cooled at the other end by a freezing mixture. This gives a fairly even gradation from 58° to 5° C. The electric coil has low, medium, and high adjustment, so that the temperature gradient in the trough can be increased or diminished as desired. Three such thermostats were in use at one time.

The seedlings chosen for this study were *Raphanus sativus* and *Pisum sativum*. The trough was filled with sterilized *Sphagnum*. This was found to be the best medium, since in it the roots grow perfectly straight. Seeds were sown in the trough at definitely spaced intervals. When the roots were 1.5–2 cm. long, the thermostat was brought to the desired temperatures and the response

¹In work described in a very recent article, HOOKER (HOOKER, HENRY D., Thermotropism in roots, *Plant World* 17:135–153. 1914) obtained no reaction in roots set in 1.25 per cent agar. He concluded, therefore, that the curvatures of roots when grown in sawdust, as in the work of WORTMANN and KLERCKER, are due to hydrotropism. The methods of experimentation used are subject to criticism and the conclusions are erroneous.

²GANONG, W., *Plant physiology*, p. 207. 1908.

of the roots observed. In another series of experiments, seedlings grown at 20° C. were put directly into the heated thermostat.

Curvatures.—When seedlings of *Raphanus sativus* have been in the thermostat 2 hours, the roots show the following reactions:

Positive 7-15° C.	No curvature 16-23° C.	Positive 24-36° C.	Negative 38-51° C.
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At the higher temperatures the curvature occurs very quickly. Roots grown at 20° C., when put into the thermostat at 45° C., give a positive curvature in 5 minutes. This quickly goes over into a negative curvature, so that within 20 minutes there is a strong negative curvature. The explanation of this double curvature, of course, is that as the temperature of the root rises to 38° C. there is a positive curvature; when the root temperature has reached 45° C., a negative curvature begins. It should be remembered that the side of the root toward the hot end of the thermostat is always at a slightly higher temperature than the opposite side. At the lower temperatures the roots react less rapidly, requiring 1.5-2 hours for complete reaction at 7-15° C.

TABLE I
THERMOTROPIC CURVATURES OF ROOTS

	Positive	No curvature	Positive	Negative
1. <i>Raphanus sativus</i>	7-15° C.	16-23° C.	24-36° C.	38-51° C.
2. <i>Pisum sativum</i>	8-15° C.	17-29° C.	34-50° C.
(WORTMANN).....	8.5-31° C.	34-50° C.
3. <i>Sinapis alba</i> (KLERCKER)	14-29° C.	None
4. <i>Helianthus annuus</i>
(KLERCKER).....	None	15-40° C.
5. <i>Phaseolus multiflorus</i>
primary roots (WORT-	None	8-22° C.	22-50° C.
MANN).....
6. ———, secondary roots
(WORTMANN).....	10-?° C.*	?-40° C.*

* WORTMANN obtained positive curvatures at 10° C. and negative curvatures at 40° C., but made no investigations at the intermediate temperatures.

The roots of *Pisum sativum* are less sensitive to temperature changes than those of *Raphanus sativus*. After one hour in the thermostat all the roots at temperatures from 34° to 50° C. showed negative curvatures; and in 2.5 hours 80 per cent of those at

temperatures from 8° to 15° C. gave positive curvatures. At the temperatures from 17° to 29° C. there were no curvatures even after 9 hours.

Table I gives the thermotropic curvatures of five species, selected to show the various "types" of reaction. Where the data have been obtained by other workers, the name is given in parentheses.

In attempting to locate the mechanism of thermotropic curvatures, one must bear in mind the various possibilities, or "types" of reaction, shown in the table. The rapidity of the reaction indicates that it is not a growth phenomenon. It is known that the permeability of protoplasm increases with increase of temperature. The range of permeability change was not known, nor was it known whether there is such great variation with species as would be necessary to explain the curvatures given in table I. However, permeability changes and consequent turgor changes were considered a possible factor; accordingly the permeability of the roots at temperatures from 10° to 40° C. was determined for the five species.

II. Permeability

EFFECT OF TEMPERATURE ON PERMEABILITY

In 1902 RYSSELBERGHE (8) found that the permeability of the protoplasm of epidermal cells of *Tradescantia discolor* to dissolved substances (glycerine, potassium nitrate, and urea) increases with the temperature from 0° to 30° C. In 1905 LEPESCHKIN (3) found that the volume of liquid extruded by hairs on the leaves of *Phaseolus multiflorus* increases from 0° to 20° C., and decreases from 20° to 35° C. During the extrusion the osmotic pressure of the cell sap decreases, indicating an increased permeability to solutes as well as to water. In 1908 LEPESCHKIN (4, 5, 6) established the fact that pulvinal movements of leaves are due to the effect of light on the permeability of the protoplasm of the pulvinal cells. Light increases the permeability, with consequent decreased turgor pressure (decrease of volume). Darkening decreases the permeability, with consequent increase of turgor pressure (increase of volume). In 1910 TRÖNDLE (9) found that the leaves of *Buxus sempervirens* are more permeable to sodium chloride in light than in darkness;

also with a 32 C.-P. electric lamp as light source, he found an increase of permeability up to a certain light intensity (50 cm. from the lamp), and then a decrease at the higher intensities (35-10 cm. from the lamp).

METHOD

The method for determining permeability is essentially that of LEPESCHKIN (6). This method is based on the fact that the permeability of protoplasm to sucrose does not change under varying conditions, while the permeability to potassium nitrate does change. That is, with increasing permeability, higher concentrations of potassium nitrate are required to produce plasmolysis.

Weight molecular solutions were used throughout; the percentages in any series varied by 0.02 mol. The tests of permeability at the temperatures from 20° to 50° C. were carried on in a constant temperature oven, electrically controlled; those below 20° C., in an ice chest. Of course, all were in darkness. Seeds were germinated on filter paper in large Petri dishes. When the roots were about 1.5 cm. long, they were put in covered watch glasses containing the solutions and left for 20 minutes. Then they were put on a slide in a drop of the solution and observed as quickly as possible.

Repeated examination of sections of roots plasmolyzed at various temperatures showed that the degree of plasmolysis of the root hairs is an exact indication of the degree of plasmolysis of the cortical cells of the root. When the protoplasm is slightly drawn back from the tip of the root hair, the outer two rows of cortical cells are slightly plasmolyzed. When the protoplasm of the younger root hair is beginning to break up into several parts, the walls of all the cortical cells of the corresponding part of the root are slightly shrunken. In complete plasmolysis the protoplasm of the root hairs is rounded up into three or four parts, and the cortical cells are plasmolyzed. The criterion then for slight plasmolysis of the root is that condition of the root hair in which the protoplasm is slightly drawn back from the tip.

DATA

The effect of temperature on permeability is shown in the accompanying figures. The ordinates give the percentage weight-

molecular solution which produces slight plasmolysis. The increase or decrease of permeability with change of temperature is shown by the increase or decrease of these concentrations, the plasmolyzing concentration of sucrose remaining constant.

The permeability of roots of *Raphanus sativus* (fig. 1) increases from 10° to 18° C.; does not change from 18° to 24° C.; increases

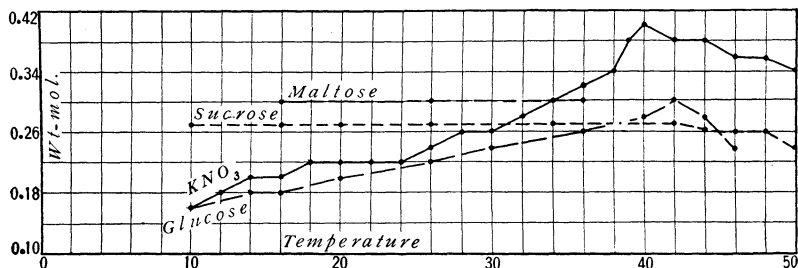


FIG. 1.—*Raphanus sativus*: curves showing the effect of temperature on the permeability of roots to potassium nitrate and glucose; ordinates indicate the percentage wt.-mol. solutions producing slight plasmolysis; dots indicate temperatures at which determinations of plasmolysis were made.

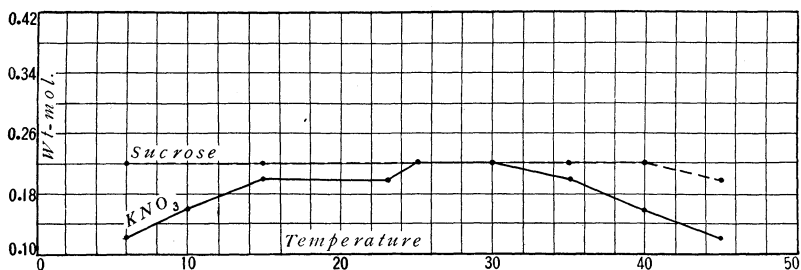


FIG. 2.—*Pisum sativum*: the potassium nitrate and sucrose curves are identical from 25° to 30° C.

from 24° to 40° C., and then decreases. The turning point in permeability to glucose is at 42° C. The drop in the sucrose curve above 42° C. suggests a decreased osmotic pressure due to exosmosis. To test this, roots were put in distilled water at 45° C.; after 20 minutes the water gave a sugar test with Fehling's solution. Thus at 42° C. there is an increased permeability, in all probability caused by coagulation of the protoplasm.

The permeability of roots of *Pisum sativum* (fig. 2) to potassium nitrate increases from 6° to 15° C.; does not change from 15° to

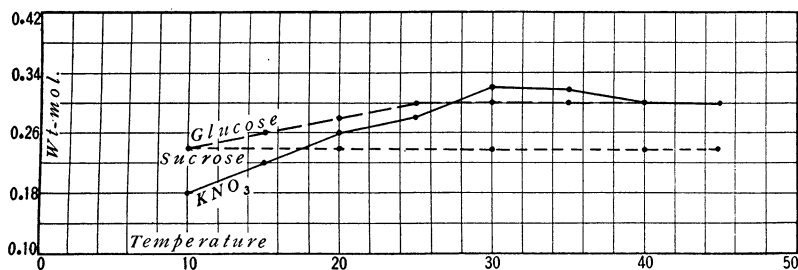


FIG. 3.—*Sinapis alba*: the potassium nitrate and glucose curves are identical from 40° to 45° C.

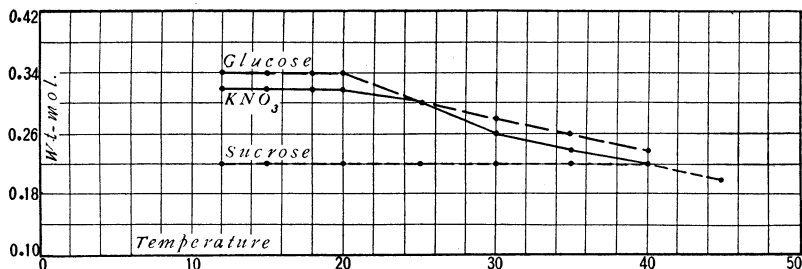


FIG. 4.—*Helianthus annuus*: the potassium nitrate and glucose curves are identical from 40° to 45° C.

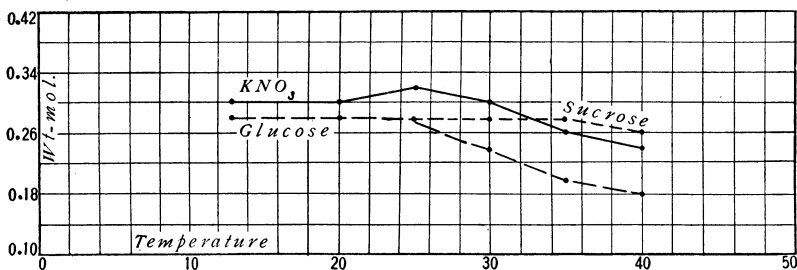


FIG. 5.—*Phaseolus multiflorus*: primary roots; the sucrose and glucose curves are identical from 15° to 25° C.

23° C.; and decreases from 30° to 40° C. The sucrose curve shows that the osmotic pressure is lower at 45° C. than at 40° C.

The permeability of *Sinapis alba* (fig. 3) increases from 10° to 25° or 30° C., then remains practically constant to 45° C.

Helianthus annuus (fig. 4) shows no increase in permeability with increase of temperature, but a decrease from 20° to 40° C.

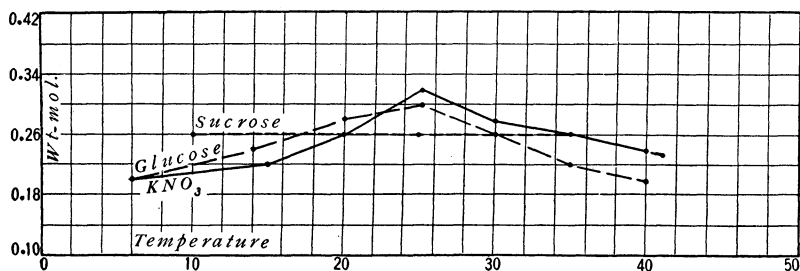


FIG. 6.—*Phaseolus multiflorus*: secondary roots; the potassium nitrate and sucrose curves are identical from 35° to 40° C.

The primary roots of *Phaseolus multiflorus* (fig. 5) show no increase in permeability from 13° to 25° C.; while in the secondary roots (fig. 6) the permeability increases from 6° to 25° C. Both have a decreasing permeability from 25° to 35° C.

COMPARISON OF THERMOTROPIC CURVATURES AND PERMEABILITY CHANGES

To show the relation between thermotropic curvatures and permeability changes, the data given in table I are given in table II

TABLE II

THERMOTROPIC CURVATURES AND PERMEABILITY VARIATIONS OF ROOTS

		+	o	+	—
1. <i>Raphanus sativus</i> . . .	{ Curvatures	7-15° C.	16-23° C.	24-36° C.	38-51° C.
	{ Permeability	10-14° C.	18-24° C.	24-40° C.	40-50° C.
2. <i>Pisum sativum</i>	{ Curvatures	8-15° C.	17-29° C.	34-50° C.
	{ Permeability	6-15° C.	15-35° C.	35-45° C.
3. <i>Sinapis alba</i>	{ Curvatures (K)	14-29° C.	None
	{ Permeability	10-30° C.	30-45° C.	None
4. <i>Helianthus annuus</i> . .	{ Curvatures (K)	None	15-40° C.
	{ Permeability	None	12-20° C.	20-40° C.
5. <i>Phaseolus multiflorus</i> (primary roots) . . .	{ Curvatures (W)	None	8-22° C.	22-50° C.
	{ Permeability	None	13-20° C.	25-40° C.
6. ——— (secondary roots)	{ Curvatures (W)	10-2° C.	?-40° C.
	{ Permeability	6-25° C.	25-40° C.

together with the temperatures at which there is increasing or decreasing permeability, for each species. In the table, + indicates positive curvatures and increasing permeability; o indicates no curvatures and no change in permeability; — indicates negative curvatures and decreasing permeability.

The data show that the permeability increase or decrease parallels almost exactly the positive or negative curvatures. In every case, at those temperatures which cause positive curvatures there is increasing permeability; where there are no curvatures, there is no change in the permeability; and at temperatures causing negative curvatures there is decreasing permeability. The slight differences in temperature at the turning point are well within the range of experimental error.

Conclusions

WORTMANN'S inability to obtain positive thermotropic curvatures in the primary roots of *Phaseolus multiflorus* is explained by the fact that there is no increase in permeability. In the secondary roots, however, where he found positive curvatures, there is an increasing permeability. KLERCKER obtained no negative thermotropic curvatures in *Sinapis alba*; there is no decreasing permeability. Also, KLERCKER obtained only negative curvatures in *Helianthus annuus*; there is no increasing permeability, therefore no positive curvatures.

The permeability of the cells of the root to potassium nitrate and to glucose increases or decreases with increase of temperature according to the species, and for a given species according to the temperature.

With unequal temperature on opposite sides of a root, a curvature is produced only when the cells of the root are more permeable at one of the temperatures than at the other. Those cells which are subjected to a temperature at which they are more permeable to dissolved substances are consequently less turgid. This results in a shrinking of the tissues on that side of the root and a consequent mechanical curvature. Always the more permeable side of the root becomes concave.

Summary

1. Thermotropic curvatures of roots vary with the temperature and with the species.

2. Permeability of the cells of the root to dissolved substances varies with the same factors.

3. In every case the greater permeability is in the concave side of the root; where the thermotropic reaction of the root changes, the permeability also changes.

4. The parallelism between the permeability and thermotropic reaction is exact; turgor change produced by permeability change offers a mechanical explanation of the curvature.

5. Heat does not act as a stimulus, but by affecting permeability as a direct factor producing curvature; hence, thermotropism is not a tropism, but is a turgor movement.

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